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Life History of a Dune-Dwelling Rhaphidophorid, Utabaenetes Tinkham, in the San Rafael Desert of Utah

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LIFE HISTORY OF A DUNE-DWELLING RHAPHIDOPHORID,

UTABAENETES TANNERI TINKHAM, IN THE

SAN RAFAEL DESERT OF UTAH

being

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by

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PREFACE

This thesis is written in the format appropriate for publication in the Annals of the Entomological Society of America.

ABSTRACT

The camel cricket, *Utabaenetes tanneri* Tinkham, has been little studied. This study gathered information on the basic life history and behavior of this species, which is found only in the San Rafael Desert and adjacent Colorado Plateau in areas of loose sand or active dunes. The daily activity pattern is matutinal, and individuals construct burrows for shelter in the afternoon. The diet of *U. tanneri* is omnivorous, composed of plant material, detritus, and conspecific crickets. *Utabaenetes tanneri* has been found in the diet of several predatory species, although the total number of observed predation instances is low. *Utabaenetes tanneri* might be a Batesian mimic of sympatric tenebrionid beetles, which might explain the small number of observed predation attempts on this species.

Utabaenetes tanneri can be very abundant where it occurs. Abundance and density of crickets was determined for three study plots in Grafield County, Utah. Plot 1 had a mean abundance of 482 crickets, determined by mark and resight analyses, and a mean density of 0.23 individuals per square meter. Only one cricket was found in Plot 2, and no mark and resight analysis was performed. Plot 3 had a mean abundance of 50 crickets, and a mean density of 0.022 individuals per square meter. The bulk density of the soil was compared between the three sites, but no significant difference was found (Kruskal-Wallace $X^2 = 0.932$, df = 2, $P = 0.627$), and therefore is probably not the reason for the differences in abundances between the three plots.

Studies on similar species of sand treaders have indicated that they are important detritivores within arid ecosystems. They are also preyed on by numerous species, and are usually one of the most abundant arthropods where they occur. *Utabaenetes tanneri* probably functions in a similar ecological role to these other species of sand treaders.

In addition to these observations of *U. tanneri*, a morphological description of the species is provided. The first key to the subfamilies of Rhaphidophoridae in the United States and Canada is presented, along with a key to the genera of the subfamily Ceuthophilinae.

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INTRODUCTION

The Insecta might be the most speciose clade of animals on the planet, with over 827,000 described species (Polis 1991a, Kim 1993) and an estimated total species richness from 5 to 8 million species (Gaston 1991, Polis 1991a, Wilson 1992, Kim 1993), out of a total projected global biodiversity between 10 and 30 million species (Kim 1993). These estimates are conservative; Erwin (1988) predicted that there were over 30 million species of insects alone.

The biomass of insects, and other arthropods, comprises the bulk amount of biomass for consumers in most terrestrial ecosystems worldwide (Kim 1993). They are an important component of most terrestrial food webs (Bradley 1983, Polis 1991a, Megías et al. 2011); because of this, insects have an enormous impact on their environment (Miller 1993). In resource-limited ecosystems, such as deserts, this is especially true (Bradley 1983, Megías et al. 2011).

The Orthoptera are key components in the ecology of arid environments (Rodell 1977, Bradley 1983, Crawford 1991, Schoenly et al. 1991). They are consumers across several trophic levels; species are herbivorous, predaceous, omnivorous, or macro-detritivores (Rodell 1977, Bradley 1983, Crawford 1991, Schoenly et al. 1991) and their biomass might be much greater than that of other arthropods in the same environment (Gandar 1982). Some species are comparatively well studied; these tend to be species of direct economic importance, such as the Mormon cricket (*Anabrus simplex* Haldeman), a tettigoniid (MacVean 1990), and the Great Plains camel cricket (*Daihinia brevipes* Haldeman)

(Whitehead and Miner 1944), a rhaphidophorid, both of which are crop pests. Other species of Orthoptera that lack economic impact still perform important ecological roles, but these have been comparatively little studied (Hubbell 1936, Tinkham 1970, Polis 1991a, Weissmann 1997).

One of the most abundant insect groups on desert dunes are orthopterans of the family Rhaphidophoridae (Crawford and Taylor 1984), members of which are known as cave or camel crickets. This family contains approximately 165 species in the United States and Canada (Eades et al. 2012, Shofner unpubl. data), and is distributed widely across the continent in diverse habitats (Hubbell and Norton 1978, Weissmann 1997). These crickets are apterous, and lack tympana and the specialized morphology used to produce songs.

Most researchers have focused on troglobytic species within this family (Hubbell and Norton 1978, Lavoie et al. 2007), resulting in a relative dearth of information on arenicolous species, or "sand treaders." These species are specially adapted for life in sandy environments. Sand treaders possess specialized spination on the pro- and metatibiae, which is used to burrow into loose sands. Most species of sand treaders are nocturnal (Tinkham 1962a, 1962b, 1970, Weissman 1997), with one notable exception, which is the focus of this study. Most information on sand treaders to this point has been provided by Tinkham (1962a, 1962b, 1970) in his series of papers on neartic sand dune orthoptera and Weissmann (1997) in his paper on the natural history of the giant sand treader (*Daihinibaenetes giganteus*

Tinkham). Bradley (1983) and Crawford and Taylor (1984) discussed the impact of a genus of sand treader (*Ammobaenetes* Hubbell) on desert ecosystems.

The dunes in the San Rafael Desert of central Utah are isolated from other dune systems in the Great Basin and other deserts, which contribute to a unique flora and fauna within the region (Tinkham 1970). Within the San Rafael Desert, two genera of sand treaders, *Utabaenetes* Tinkham and *Ammobaenetes*, inhabit interspersed dunes (Tinkham 1970). This study focuses on the life history of *Utabaenetes tanneri* Tinkham. After the original description of the species, no other paper has been published on *U. tanneri*, although Weissmann (1997) mentions the species briefly in comparison to *D. giganteus*.

METHODS

Field Observations

Observations of *U. tanneri* were conducted from 18 through 25 May and 15 through 17 August 2012, and 12 through 14 April, 18 May through 9 June, and 30 August through 2 September 2013. Cricket activity was monitored throughout the day, from before sunrise until after sunset, usually to 23:00 hours. Observations made on *U. tanneri* behaviors and interactions with the environment—such as food consumed, predation events, or reproduction—were recorded during or immediately after such events. When possible, behaviors were recorded with a digital SLR camera as photographs or videos. Approximately one meter was kept between the observer and individual crickets in an effort to ensure behavior was not disrupted. Voucher specimens were collected in 2012 and 2013 and placed in the entomology collection at the Sternberg Museum of Natural History (museum code FHSM). These specimens were used as a reference for morphological description and drawings.

Lab Observations

Eight adults, four males and four females, were collected on 25 May 2012 and kept in a 75.7 L (20 gal.) glass aquarium. They were exposed to a simulated day/night cycle with 12 hours of day and 12 of night, and observations on activity were recorded.

A late instar female was collected 14 April 2013 and kept in a Plexiglas container with several centimeters of sand at the bottom. This cricket was placed near a window, and had natural day/night cycles. The container was small and the captive cricket constructed burrows against the Plexiglas. This allowed burrowing behaviors to be observed and recorded.

Keys

Keys to the subfamilies of Rhaphidophoridae of North America and genera of the subfamily Ceuthophilinae were constructed by using the original descriptions of all groups and any re-descriptions that were available. In addition, many couplets in the key to the genera of Ceuthophilinae were adapted and modified from Caudell (1916) and Tinkham (1970), neither of which listed all genera described within that subfamily. The keys presented here are therefore the first key to the subfamilies of Rhaphidophoridae of North America and the first cohesive key to the subfamily Ceuthophilinae.

Mark and Recapture

From 31 May to 2 June 2013, mark and resight data were recorded for three study plots in Garfield County, Utah. The three study plots used for mark and resight were subjectively chosen due to their superficial difference in vegetative and soil structure. Plot 3 was located on dunes with no vegetation. Plot 2 was selected because it has a sandy substrate stabilized by dense woody vegetation. Plot 1 had characters in common with the other two plots, namely dune-like substrate of loose sand with woody vegetation present, though not as dense as in Plot 2.

The mark and resight data were used to estimate abundance of *U. tanneri* at each plot. Each plot was square, with sides 45.7 meters in length. The northwest corners of these plots were located at 38.071213, -110.547798 (Plot 1); 38.071785, -110.545291 (Plot 2); 38.072597, -110.540153 (Plot 3) (Fig. 1). Crickets were marked with enamel model paint (Fig. 2), which Weissmann (1997) used to mark *D. giganteus*. Crickets were marked with a color unique to their plot. If crickets moved outside the plot area, I could determine which plot they originated from by their markings. Many individuals were marked in Plot 1 before the final mark and recapture study (168 total) to test methods for marking crickets, resight sampling, and durability of marks.

Starting from the first cricket to emerge and lasting 1 hour from that point, individuals were marked with paint on their thorax or abdomen. Care was taken to create as little disturbance to each individual as possible to minimize impacts of marking on normal behavior. Resighting commenced immediately after marking was finished.

Each study plot had six primary transects composed of two subordinate transects within each primary transect. I started sampling at the northwest corner of each plot and moved in a straight line to the southeast corner (subordinate transect one). From there, I moved to the northeast corner, traversing outside the plot; I then sampled from the northeast corner to the southwest corner (subordinate transect two). From the southwest corner, I moved to the northwest corner, traverseing outside the plot (Fig. 3). These two subordinate transects

combined were considered one primary transect. A straight line transect was used for sampling without replacement, because the crickets did not have individually distinguishable marks. Sampling without replacement only needed to occur within each subordinate sampling effort; individuals counted within one subordinate effort could be counted again in the next effort without violating this assumption (McClintock 2013). Sampling was finished in approximately 2 hours, and always before 0900 hours, reducing the number of crickets entering or leaving the plot and minimizing the violation of the mark and resight model's assumption of closed populations.

As I moved along the transect, I counted individual crickets, and recorded the sex of individuals and whether they were marked or unmarked. Observations were separated into four groups: marked male, marked female, unmarked male, and unmarked female. Mark and resight data were recorded using the Apple Numbers application on an Apple iPod 4. GPS data were acquired using the internal GPS of an Apple iPhone 4s, and using DM Software Solutions GPS Tracks application (Morneault 2013) for navigation and storage of GPS data. GPS locations were recorded with an X/Y precision of ±2.74 m.

The mark and resight data (Tables 1 and 2) were used to construct artificial encounter histories (Tables 3 and 4). These histories represent how many marked individuals were seen in each sampling period. The encounter histories consist of coded values representing whether a marked individual was encountered (1) or not encountered (0) during a transect. For example, given four sampling periods, with

3, 2, 4, and 2 marked individuals resighted respectively, there would be two individuals with the encounter history 1111, one with the history 1010, and one with the history 0010. The code 1111 indicates that an individual was resighted every transect, while 1010 indicates that individuals with that history were seen every other transect.

To calculate abundance, these encounter histories were combined into a single encounter history, with two groups: group 1 was the encounter histories for Plot 1, and group 2 was the encounter histories for Plot 3. This combined encounter history was input into Program MARK version 7.1 (Cooch and White 2013). Abundance was calculated using the mixed logit-normal mark-resight model (McClintock 2013). This model requires the number of marked individuals in the population to be known. Models were run with a variable or fixed detection probability, p, and multiple combinations of link functions and variance estimation functions. All variations of the model were run with ∂ fixed to zero (∂ is used to calculate individual detectability heterogeneity, which can not be computed because individual identities are not known).

The top three models all had identical AIC_c values ($AIC_c = 752.0344$). There were 33 parameters for each of these models. These parameters were the estimates of p for each primary transect for plots 1 and 3. All models with any Model Likelihood value above zero were averaged, weighted by each model's Model Likelihood value, to produce the most likely estimate of abundance (Cooch and White 2013).

Site Characteristics

Plants within each study plot were identified to species, and specimens of each species were collected and prepared as museum specimens. These specimens were deposited in the Elam Bartholomew Herbarium at FHSM. Additional plant species not found in the study plots, but found in other areas where *U. tanneri* occur, also were collected, identified and prepared as specimens.

The bulk density of soil was examined to determine if soil bulk density was correlated with cricket abundance. Sixteen soil samples were taken from each of the three mark and resight study plots. The soil sample locations were distributed evenly using a regular arrangement of points generated with ESRI ArcGIS 10.1 (ESRI 2012) (Fig. 1). Soil sample location coordinates were loaded in an Apple iPhone 4s and navigated to within 1 m ±2.74 m using the internal GPS and DM Software Solutions GPS Tracks (Morneault 2013). I extracted soil samples using a 47.90 mm diameter probe pushed into the soil to a depth of 100 mm. Each sample was transferred to an individual quart size re-sealable zipper storage bag and labeled with the plot number and soil sample number. Noticeable vegetative material was removed from samples, though this was seldom needed. Mass of the soil samples was measured with a digital balance with a precision of 0.01 g. The "wet" mass of the soil was recorded, and then added to the mass of the container to produce a total mass. The soil samples were placed in a convection oven and dried at 130 °C for 24 hours. The mass of the samples was checked at 4.5 hours and 7.5 hours and the values subtracted from the total mass to track loss of water within the samples.

Bulk density was computed by dividing the dry mass of the soil by the volume of the original sample. The bulk densities of soil samples, by plot, were compared statistically. A Levene's test for homogeneity of variance across groups (df = 2, F = 3.602, P = 0.03539) was used to determine if the data fit the assumptions of variance testing. This was computed in R using the package car version 2.0-19. A Kruskal-Wallace test (R version 3.0.2 (R Core Team 2013)) was used to compare plots because the variances were not equal between plots.

Some temperature observations of the substrate surface were recorded during both field seasons by using a hand-held Nicety ST380A infrared thermometer. Climatic data for 2013 were acquired from the National Weather Service/Federal Aviation Administration weather station KHVE located in Hanksville. These data were used to estimate air temperatures at time of emergence and at the time of cessation of surface activity. Times were rounded to the nearest hour.

Remote Sensing

LandSat 8 imagery for Emery, Garfield, Grand, Kane, San Juan, and Wayne counties in Utah was acquired from the United States Geological Survey and used to determine the distribution of sand dunes in these counties. The imagery used was acquired 11 and 18 June 2013. The imagery was imported into ESRI ArcMap 10.1 (ESRI 2012) and combined using the mosaic tool into a single multi-band raster image, which was then clipped to the counties of interest. The image was then classified into 50 categories by using bands 1 through 7 and the ISO unsupervised

cluster analysis tool. The categories located on dunes ground-truthed during the study were used as a mask to extract the areas covered by these categories from the unclassified LandSat imagery. These parts of the image were then classified into 20 categories using ISO unsupervised cluster analysis. This allowed for a more refined dune extent that eliminated areas of similar colored rock formations, which the first cluster analysis had trouble distinguishing from sand. Only the categories associated with dunes were extracted and used in the final map.

DESCRIPTION OF *UTABAENETES TANNERI* AND KEYS

Description

Adult *U. tanneri* are black, and among the largest rhaphidophorids. Adults are relatively soft-bodied, and their abdomens shrivel considerably as dried specimens. The shape of the abdomen varies, as live individuals vary in the amount of distension of the abdomen, even within a single individual. Therefore, though total length and abdomen length were measured from preserved specimens, these measurements should be used cautiously given the variation in the shape of the abdomen, as well as the rounded C-shape of the body.

I measured several anatomic features on four males (Table 5) and six females (Table 6). The following description is adapted from Tinkham (1970).

Procoxae of both sexes bear spine-like projections on the forward margin; dorsal surface of profemora lacking spines; ventral surface of males with one to several minute teeth on anterior keel, six or more minute teeth on posterior keel, usually with subapical spine present; females possess reduced dentition on anterior keel, only subapical spine on posterior keel. Both sexes lack spines on dorsal surfaces of protibiae except for pair of apical spurs, with four pairs of large posteroventral spurs and large apical spur (Fig. 4b). Three protarsomeres present, with ventrodistal margin of third tarsomere shaped as rounded point.

Mesocoxae without spines, mesofemora dorsally unspined. Posteroventral mesofemora keels with four to ten teeth in males, one to four in females. Mesotibiae with four to five pairs of acuminate spurs and paired apical spurs dorsally, three to

four pairs of smaller spurs, pair of large apical spurs ventrally. Four mesotarsomeres, each with lobate distoventral angle.

Metacoxae without spines, male metafemora with two to four very large spikelike teeth and one or two small teeth apically on anteroventral keel, and several small teeth widely spaced on posteroventral keel (Figs. 4c and 4d). Female metafemora lack teeth on anteroventral keel, with reduced teeth on posteroventral keel (Fig. 4e). Dorsal surfaces of both male and female metafemora with many minute teeth. Male metatibiae appear slightly more arched than female metatibiae. Both sexes lack spines on ventral surfaces of metatibiae, except for pair of short apical spurs distally. Five pairs of acute, large, moveable spines crowded apically on dorsal surface of metatibiae, forming the "sand basket" and pair of spurs apically (Fig. 4f). Three additional sets of acute spines are located on antero- and posterodorsal keels, separated by one to four minute teeth. Spines on all tibiae with red coloration apically. Metatarsi consist of three tarsomeres, with third tarsomere acute distoventrally.

Cerci long and sparsely setose. Ovipositor slightly recurved, approximately three times longer than pronotum. Dorsal valvulae with apical spine, ventral valvulae with 6 curved hooks (Figs. 4g and 4h).

Eyes of males are often golden in color (Fig. 5), especially when exposed to artificial illumination, as seen under a microscope. This character appears to be retained even in preserved specimens. All females observed during this study had black colored eyes (Fig. 5).

Key to the Subfamilies of Rhaphidophoridae of the United States and Canada

1 All tibiae square in transverse section, similarly armed above and beneath on both outer and inner margins with short, heavy, close-set spines of equal length ..... Tropidischiinae

1’ None of tibiae at all as described. 2

2(1) Basal segment of metatarsus truncate posteriorly above or scarcely produced..... Ceuthophilinae

2’ Basal segment of metatarsus produced posteriorly above into stout spine, or tapering spinelike process 3

3(2) Pro- and mesofemora with long genicular spine on one or both sides; metafemora as long as, or longer than, body; second segment of metatarsus about as long as fourth segment exclusive of claws, two or more times as long as vertical depths. Introduced to North America, usually found near greenhouses ..... Aemodogryllinae

3’ Femora without genicular spines, femora distinctly shorter than body; second segment of metatarsus barely one-half as long as fourth, scarcely longer than vertical depths.....Gammarotettiginae

Key to the Genera of Ceuthophilinae

The below key was mostly adapted from keys by Caudell (1916) and Tinkham (1970). Genera presented in this key but not present in either original key include *Euhadenoecus*, *Farallonophilus*, and *Salishella*.

1 Sand basket present, consisting of four to six pairs of long, moveable, acute spurs, somewhat flattened on their inner faces and crowded apically on metatibia 2

1' Sand basket absent..... 7

2(1) Mesotibae with three to five pairs of dorsal spines or spurs, exclusive of apical spurs..... 3

2' Mesotibae with two pairs of dorsal spines, exclusive of apical spurs..... *Rhachocnemis* Caudell

3(2) Anterior inferior keel of metafemora untoothed; metatibiae straight. Ovipositor long, slender, about one-half the body length..... 4

3' Anterior inferior keel of metafemora toothed; teeth of variable size, sometimes very large, often smaller and uniform. Ovipositor very short to medium in length..... 5

4(3) Tarsomere ratio 3-4-4 with their distoventral angles well-rounded ..... *Daihiniella* Hubbell

4' Tarsomere ratio 3-4-3 with their distroventral angles spined or acute..... *Ammobaenetes* Hubbell

5(3) Color pale. Tarsomere distoventral angles acute. Ovipositor short, equal to length of pronotum. Metatibiae straight or curved; anterior inferior keel of metafemora with either a row of uniform teeth or with irregular, huge, spikelike teeth and smaller teeth 6

5’ Color black as adult, instars creamy-white to pale-yellow. Tarsomere distoventral angles lobate on all but third segment of metatarsi. Ovipositor long and slender with six uncinate teeth apically on the lower valvulae; length of ovipositor about half of body length. Metatibiae straight; the anterior inferior keel of metafemora with one to three huge, spikelike teeth widely seperated and with several smaller teeth .... *Utabaenetes* Tinkham

6(5) Metatibiae strongly arched in males. Anterior inferior keels of metafemora with a row of strong uniform teeth ... *Macrobaenetes* Tinkham

6’ Metatibiae straight in both sexes. Anterior inferior keels of the metafemora with two to four very large, spikelike teeth centrally situated on keel, preceded and followed by smaller teeth .... *Daihinibaenetes* Tinkham

7(1) Eyes present; widespread 8

7’ Eyes absent; from Florida ..... *Typhloceuthophilus* Hubbell

8(7) Tarsal claws with a distinct ventroproximal sensory seta; male subgenital plate entire or distally emarginate, not divided into lateral halves by a

median cleft or fold; ventral valves of ovipositor armed distally with crennulations or numerous low serrations..... 9

8’ Tarsal claws without trace of ventroproximal sensory seta; male subgenital plate divided into lateral halves by median fold or cleft, sometimes undivided; ventral valves of ovipositor armed with 4 to 8, often 5, triangular or aciculate teeth (including the decurved, hook-like apex), these rarely serratiform or subobsolete.....13

9(8) Fastigium of vertex small, deeply sulcate or bifid; all femora unarmed; moveable dorsal spurs of metatibia variable in number, irregularly spaced but normally separated by four or more times their own length; male cerci simple, attenuate; legs extremely long and slender.....10

9’ Fastigium of vertex convex to conical, not sulcate or bifid; metafemur armed with spine at knee or all femora unarmed; moveable dorsal spurs normally 5 or 7 on each carina, or absent; male cerci occasionally specialized; legs of moderate length, occasionally stout.....11

10(9) Male with a pair of pale membranous glandular areas at sides of epiproct and without eversible tubular organs between 9th and 10th tergites; subgenital plate trapezoidal, with distolateral portions set off by oblique sulci and bearing small socketted styles; paraprocts with ends little decurved, narrow and incurved or bulbous. Female subgenital plate

without intramarginal sclerite; ovipositor teeth without distal process. Metafemura without genicular spinule. Legs relatively shorter..... .....*Euhadenoecus* Hubbell and Norton

10’ Male without pale areas at sides of epiproct; a pair of fleshy elongate tubular organs protrusible from slits between 9th and 10th tergites anterior of cercal bases; subgenital plate subtriangular, terminating in a pair of subconical lobes bearing small, partly fused styles at their tips; paraprocts more or less strongly decurved distally, their apices in side view broad and subplanate or narrowed to ventrally projecting points. Female subgenital plate with an intramarginal ventral sclerite; ovipositor teeth with a minute hair-like process extending distally from their distoventral angles. Metafemura nearly always with a minute spinule at knee. Legs relatively longer..... *Hadenoecus* Scudder

11(9) Pulvilli of first two tarsal joints broad throughout; fastigium convex and not prominently conical.....*Salishella* Hebard

11’ Pulvilli extending proximally from apex as a narrow ventral keel; fastigium prominent and conical 12

12(11) All femora unarmed; restricted to Farallon Islands of California..... .....*Farallonophilus* Rentz

12’ Femora with at least some armament, occasionally heavily so; widespread in the southwest and west coast United States..... .....*Pristoceuthophilus* Rehn

13(8) Tarsal formula 4-4-4; mesofemoral genicular spur present, usually well-developed.....14

13’ Tarsal formula either 3-4-3 or 3-4-4; mesofemoral genicular spur reduced or absent.....16

14(13) Dorsal surface of protibiae unarmed except at apex.....15

14’ Dorsal surface of protibiae with stout spur slightly distal of middle of anterior margin .....*Udeopsylla* Scudder

15(14) Dorsocaudal apical spur of metatibiae but little longer than last dorsal spur and usually less than 1.5 times as long as ventrocaudal apical spur; dorsal margins of metatibiae with more or less reduced number of denticulations, anterior carina with 0 to 24 in all, and with 0 to 12, often fewer than 5 proximally of first spur, rarely as many as 5 and often only 2 to none in remaining intervals, especially distally; proximal spurs stout, cylindroconic, straight, or weekly curved, with delicately unicarinate dorsal surface, distal spurs similar but longer; ventrodistal half of metatibiae with 3 to 8, usually 4 to 5 spurs in addition to apical pair, these usually partially biserate distally; foreleg distinctly more robust than middle leg, protibae somewhat swollen, especially distally, and ventral spurs heavy; fastigium depressed, subplanate, apex usually with a faintly impressed median line .....*Styracosceles* Hubbell

15’ Dorsocaudal apical spur of metatibiae usually much longer than last dorsal spur and ventrocaudal apical spur (rarely less than 1.5 times as

long as latter); dorsal margins of metatibiae with variable but normally large number of denticulations, anterior carina with 17 to 62 in all, usually with more than 25 and very rarely with less than 20, space proximally to first spur with 4 to 25, usually more than 10 and rarely fewer than 6, remaining intervals with larger average number than *Styracosceles* (if denticulations unusually few, then dorsocaudal apical spur at least 1.5 times as long as last dorsal spur, and/or ventrocephalic carina of profemura nodulose); dorsal spurs usually slender and relatively elongate, flexor surface commonly wedge-shaped in section, dorsal surface with a pair of delicate parallel carinae or with one such carina, extensor surface commonly setose, apex usually incurvate and/or minutely and abruptly in-bent at tip (dorsal spurs of some species occasionally resembling proximal spurs in *Stryacosceles*, in which case intervals multispinose, or tarsi elongate and dorsalcaudal apical spur much longer than last dorsal spur and ventrocaudal apical spur, or fastigium distinctly prominent; distal spurs and apical spurs never or only rarely blade-like toward apices); distrovental surface of metatibiae with 0 to 5, usually 1 or 2 small spurs in addition to actual pair..... ..... *Ceuthophilus* Scudder

16(13) Tarsal formula 3-4-4 (metatarsi in *Phrixocnemis* showing incipient fusion) 17

16’ Tarsal formula 3-4-3 ..... *Daihinia* Haldeman

17(16) Dorsal margins of metatibiae with 5 spurs (exclusive of apical spurs), interval between two distal spurs of anterior margin more than twice the width of one spur; protibiae but moderately enlarged, its ventral and distal spurs present but not unusually developed, dorsocaudal spur straight, aciculate, considerably smaller than ventrocaudal distal spur; each dorsal carina of mesotibiae usually with 2 spurs; apices of lobes of male subgenital plate moderately prolonged.....*Phrixocnemis* Scudder

17' Dorsal margins of caudal tibia with 7 spurs (exclusive of the apical spurs), interval between two distal spurs of anterior margin not or scarcely wider than the width of one spur; protibiae strongly swollen, especially in distal two-thirds, its ventral and distal spurs very large and heavy, the dorsalcaudal thickened and curved, similar to and but little smaller than ventrocaudal distal spur; each dorsal carina of middle tibia usually with 4 spurs; apices of lobes of male subgenetial plate strongly produced..... ..... *Daihiniodes* Hebard

LIFE HISTORY OF *UTABAENETES TANNERI*

Habitat

Locations where *U. tanneri* occur can be characterized by the presence of loose fine-grained sand. These locations range from active dunes devoid of vegetation to scrubland with loose sands. Bulk density of the soil was recorded for three study plots (Table 7). There was not a significant difference between the bulk densities of the three plots (Kruskal-Wallace $X^2 = 0.9324$, df = 2, $P = 0.6274$) (Fig. 6).

Dominant vegetation where *U. tanneri* occurred includes purple sage (*Poliomintha incana* (Torr.) A. Gray), Thompson's indigo-bush (*Psorothamnus thompsoniae* var. *thompsoniae* (Vail) S.L. Welsh and N.D. Atwood), and sandhill muhly (*Muhlenbergia pungens* Thurb. ex A. Gray). Other common species include sand sagebrush (*Artemisia filifolia* Torr.), Mormon tea (*Ephedra viridis* Coville), resinbush (*Chrysothamnus stylosus* (Eastw.) Urbatsch, R.P. Roberts and Neubig), Havard's oak (*Quercus havardii* Rydb.), Harriman's yucca (*Yucca harrimaniae* Trel.), sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), and Indian ricegrass (*Achnatherum hymenoides* (Roem. and Schult.) Barkworth). Desert sunflower (*Helianthus anomalus* S. F. Blake) and prairie sunflower (*H. petiolaris* Nutt.) commonly are found on otherwise bare dunes. Two uncommon but noticeable species found in *U. tanneri* habitat are Utah juniper (*Juniperus osteosperma* (Torr.) Little) and the invasive tamarisk (*Tamarix chinensis* Lour.).

Other sympatric Orthoptera included two rhaphidophorids: an undescribed species of *Ammobaenetes* (Tinkham 1970), and an unidentified member of *Ceuthophilus.* Also present were a species of stenopelmatid, a tettigoniid, Gillette's shieldback (*Plagiostira gilletti* Caudell), and two acridids: the toothed dune grasshopper (*Trimerotropis agrestis* McNeill) and the alkali grasshopper (*T. salina* McNeill) (Tinkham 1970).

Geographic Range

Utabaenetes tanneri is endemic to the Colorado Plateau. During this study, *U. tanneri* were detected in Emery, Wayne, and Garfield counties of southeast Utah. Tinkham (1970) collected specimens from both the San Rafael Desert (Emery and Wayne counties), and the Escalante Desert (Kane County). The species is likely confined to the San Rafael and Escalante deserts, west of the Green River, north of the Colorado River, and east of the Wasatch Range, Henry Mountains and the San Rafael Swell (Fig. 7). These geographic features might be barriers to dispersal of *U. tanneri*. Fig. 8 depicts the distribution of appropriate sandy habitat in the region, where *U. tanneri* might occur. More observations are needed to determine the exact range of the species.

Activity

Adult *U. tanneri* were observed between late April and mid June. Tim Graham (personal communication) found individuals as late as mid-July, while Tinkham (1970) did not find any individuals during a survey in late July. No individuals were observed in August during this study. Adults began emerging from

burrows approximately 15 minutes before sunrise each day. The earliest observed emergences were between 05:28 hours (June 7 2013 with sunrise at 05:59 hours) and 05:45 hours (May 29 2013 with sunrise at 06:02 hours). Individuals emerged from their burrows occurred at a wide range of temperatures, from -0.33 °C to 15 °C surface temperature, and from 5 °C to 25 °C ambient temperature. Most individuals sat at the entrance to their burrow for several minutes before moving away from the entrance, while others would immediately move several centimeters to several meters from their burrow before sitting still for several minutes. Some individuals sat under shrubs or leafy forbs, but others sat exposed on bare sand, even if cover was available nearby. A few individuals forewent this period of inactivity on the surface and immediately started moving.

An additional behavior observed only at the beginning of the activity period was that some males would rub the underside of their abdomens on the surface of the sand laterally back and forth over several meters, leaving distinctive and noticeable tracks in the sand (Fig. 9). Some burrows had several of these tracks leading from the burrow. It is unknown whether the same male made each of these tracks, or if there were multiple males occupying the same burrow; however, multiple individuals were never observed emerging from the same burrow. Neither males nor females reacted to these tracks in any noticeable way; individuals of either sex that encountered tracks did not follow the tracks nor did they stop and probe the tracks with their antennae. However, individuals crossed these tracks during their movement.

Surface-active individuals moved in two different patterns: movement in a singular direction, or a somewhat circular pattern or wandering path. In both patterns, individuals constantly evaluated their surroundings with their antennae by moving them continually over the substrate throughout their range of motion, stopping to investigate potential food items; males additionally investigated other crickets they encountered, while females did not usually react to the presence of other crickets unless approached by a male that was attempting to copulate. During their active period, some crickets stopped moving (even ceasing the movement of their antennae, which they otherwise move when they sit in one location for a short time), and sat for one to several minutes either under cover or exposed on bare sand. Individuals on bare sand were observed sitting in both sunlight and shadow cast by either dunes or vegetation. One individual sat and rotated to face different directions for 3 minutes on two different occasions over the course of one morning.

By 09:00 hours, some individuals began construction of burrows. The first individuals to start burrowing during the day appear to be predominantly females. Males and females both investigate burrows constructed by other individuals, and some males were observed ejecting original occupants of a burrow, regardless of the sex of that individual. In some cases, the aggressor also abandoned the burrow shortly after the original occupants are dislodged. Occasionally, the aggressor was driven out, and the original occupant retained the burrow. The last individuals to enter burrows were predominantly males; few females are observed on the surface

after 10:00 hours, and most individuals ceased surface activity by 12:00 hours. The air temperature at the cessation of activity ranged from 19 °C to 36 °C.

The activity of a male was recorded over a period of 1 hour 15 minutes, beginning with its emergence (Table 8).

The activity pattern of eight captive individuals appeared dependent on light. Crickets were active when there was light, but as soon as the light was no longer available, the crickets ceased activity. Some individuals failed to construct burrows, and would remain still in the same position on the surface until light was available again.

Burrow Construction

After locating a potential site for a burrow, crickets dug into the substrate by using their forelimbs by extending both limbs at the same time and drawing them back underneath the body. The enlarged spines on the lateral edge of the protibiae aided the movement of substrate, which was piled under the thorax and abdomen. After piling sand under the body several times, the cricket moved forward slightly, with the head pressed into the substrate, and brought the hind legs forward, kicking the sand back a distance up to five times the length of the body (measured from first instars, adults might kick sand further), usually alternating hind legs. This was aided by the dual rows of enlarged spines on the distal posterior edge of the metatibiae (the "sand-basket"). The digging proceeded at a slight downward angle until a burrow began to form. Burrowing behavior from within the burrow was observed with a captive late instar. Within the first few centimeters of the burrow,

the cricket continued the behavior as before, though the use of the hind legs was minimized inside the burrow. Instead, the cricket used the forelimbs to drag the pile of substrate backwards towards the entrance, where it then used its hind limbs to expel the pile from the burrow entrance. This activity created distinctive piles of sand in front of burrow entrances.

After excavating several body lengths, the cricket ceased expelling the pile of sand from the burrow, and began to seal the entrance. The forelimbs were used as before, but now the hind limbs shoved the sand into a pile behind the cricket, which eventually formed a plug (Fig. 10). The cricket intermittently used the hind limbs to pack the soil by gently tamping it with the distal end of the metatibiae and the metatarsi. The sand-baskets were not used except to add material to the roof of the burrow. This behavior of sealing the burrow might be limited by the moisture content of the substrate, which does not adhere well to itself when dry. Some burrows collapse, at which point the burrow was usually abandoned and another started. When emerging from a burrow in the morning, the original entrance is not used. Rather, crickets emerge from a different location, constructing a new entrance in the process.

On 1 June 2013 the first individuals active at dusk were observed. These individuals emerged around 20:00 hours (sunset at 21:12 hours); both sexes were represented, though few individuals were encountered. These individuals remained active until 22:00 hours. Crepuscular emergences were observed on subsequent days in June.

Very little information was obtained on the instars of *U. tanneri*, because only three instars were seen during this study. One final instar was collected from a freshly excavated burrow at 09:30 hours on 13 April 2013, at a soil surface temperature of 20.5 °C and an air temperature of 17 °C. First instars were located on 8 June 2013 at 06:40 hours by excavating freshly constructed burrows that appeared similar to that of adult *U. tanneri* but were smaller, white in color, with black antennae. Tim Graham (personal communication) has found many nymphs active at night in March and April; no nymphs were seen active on the surface in this time period during this study, although efforts were made to locate them.

Reproduction and Growth

The mating system of *U. tanneri* appeared to be promiscuous; males and females were seen to mate opportunistically and individuals might have multiple partners. There appeared to be no courtship preceding copulation. Males attempted to mate with nearly all females they encountered. Some of these encounters led to mating, while others did not. On occasions when the female rejected the male, the female usually ignored the male, and rarely would kick the male with her hind legs.

Upon detecting a female, males spun 180 degrees and walked backwards towards the female, probing with his abdomen for the female's abdomen. If the female was receptive, she also spun around and backed into the male. When the abdomens touched, the male twists the distal end of his abdomen approximately 90 degrees, inserting his aedeagus. After mating, the crickets separated and ceased

interaction with each other. The entire process, from first detection of each other to separation, lasts 10 to 12 seconds (Fig. 11).

When males encountered other males, a brief period of combat might occur. One, or both, of the males would turn so that their hind legs were directed at the other male; this behavior appears similar to the movement associated with mating. The male then kicked at the other male with his hind legs. These interactions usually lasted 3 to 5 seconds, after which one or both of the males moved away from the location of the conflict. This behavior takes place either in and around a burrow, or while moving and foraging away from burrows. In one observation, a male backed into the entrance of a burrow and kicked the male that was excavating it. The male digging the burrow did not react to this invasion, though the interaction lasted about 10 minutes. The invading male eventually left the burrow.

Oviposition and eggs were not observed in this study. Whitehead and Miner (1944) observed *Daihinia brevipes* laying its eggs in burrow walls, while Tinkham (1962b) found a single Arizona giant sand treader (*Daihinibaenetes arizonensis* (Tinkham)) laying eggs on the surface of the substrate. Weissmann (1997) suggested that *D. giganteus* might lay eggs in the walls of a burrow because of the arid climate of their habitat in the Great Sand Dunes of Colorado, but found no evidence of this. It is possible that *U. tanneri* laid its eggs in burrows, since no oviposition was detected on the surface during this study. Approximately 25 burrows of *U. tanneri* were excavated, but no eggs were detected. However, due to

the behavior of *U. tanneri* plugging burrows, the burrows were difficult to trace, and the entire length of the burrows was not revealed.

First instars (approximately 5 mm total length) were detected on 8 June 2013. The presences of final instars observed in April indicate that at least some nymphs overwinter and undergo their final molt in April or May of the next year. No nymphs were observed from early May until early June. No adults were observed on the surface after late July. Additionally, Tinkham (1970) and Tim Graham (personal communication) did not find any individuals after mid to late July.

Abundance

Within appropriate habitat, *U. tanneri* can be abundant, and it is not uncommon to see several individuals in close proximity, usually under vegetative cover. Adults are easily located, and an observer can see dozens of individuals when standing in one location (aided by their dark black coloration against the sand).

More males than females were marked in both Plot 1 and Plot 3, although their separate abundances were not determined. Only one individual was encountered in Plot 2 during this survey; there was not enough data to run an analysis for this plot, and it is therefore excluded. Crickets were never seen far from their original plots during this study, and none were seen in plots other than the plot where they were first marked. Plot 1 had a mean abundance of 482 (range = 316, σ = 108.358) individuals over an area of 2090 m^2, and Plot 3 had a mean abundance of 50 (range = 56, σ = 20.670) individuals over 2090 m^2 (Table 9). The crude density of Plot 1 is 0.23 individuals per square meter, or one individual for

every 4.3 square meters. The crude density for Plot 3 is 0.024 individuals per square meter, or one individual for every 41.6 square meters. This indicates that Plot 1 was approximately ten times as dense a population as Plot 3.

Diet

Utabaenetes tanneri appear to be omnivorous. They were observed consuming plant matter, carrion, dung, other insects, and cannibalizing conspecifics. Individuals actively forage for food, and investigate potential food items that come in contact with their antennae. Some individuals climb into shrubs to forage, consuming buds, flowers, and leaves; this was observed on Mormon tea (*E. viridis*), resinbush (*C. stylosus*), purple sage (*P. incana*) and Thompson's indigo-bush (*P. thompsoniae* var. *thompsoniae*). Many individuals were observed feeding on Indian ricegrass (*A. hymenoides*), either climbing up into a clump to consume fresh material, or feeding on the litter of this species. Many parts of plants were eaten, including culms, blades, and caryopses. Several individuals were observed feeding on the needles and female cones of Utah juniper (*J. osteosperma*) (which are fleshy and berry-like; male cones were not observed as part of the diet). A single male was observed feeding on cattle dung.

Individuals fed on corpses or incapacitated individuals of *U. tanneri*, although none were observed capturing or feeding on healthy individuals. On one occasion, several individuals fed on the same corpse. On three occasions, individuals were seen feeding alongside tenebrionid beetles on *U. tanneri* corpses. On one of these occasions, a male was observed feeding with a tenebrionid on a decapitated female.

A few minutes later, the male stopped feeding and attempted to copulate with the corpse. After this attempt, the male returned to feeding on the corpse, but would continue to alternate between feeding on and attempting to mate with the corpse.

One foraging individual disturbed several ants, one of which latched its jaws to the front leg of the cricket. The cricket consumed the ant.

One peculiar "food item" attracted numerous *U. tanneri*. On more than one occasion, individuals chewed, and appeared to ingest, the rubber on the sole and sides of my shoes. Whenever the antennae of an individual came into contact with a shoe, that individual would stop and investigate the shoe. When I was preoccupied, my shoes would attract a number of *U. tanneri*, and there would be half a dozen on the shoes when I chanced to look down. These individuals took some persuasion to remove, and they did not react even when nudged with a finger.

Food items might be dragged or carried up to several meters. One individual was seen dragging the carcass of another *U. tanneri*, while several observations were made of individuals dragging parts of Indian ricegrass. One female was observed attempting to drag the culm and inflorescence of Indian ricegrass into a burrow.

Predators and Defense

Despite the abundance of *U. tanneri* where they occur, and a similar abundance of potential predators, notably squamates, few predation events were observed. The western whiptail (*Aspidoscelis tigris* (Baird and Girard)) and desert spiny lizard (*Sceloporus magister* Hallowell) were both seen preying on *U. tanneri*. A

lizard scat consistent in size for either of these two species was found to contain a single *U. tanneri*. A scat of a coyote (*Canis latrans* Say) was found to contain predominantly *U. tanneri* (Fig. 12) (coincidentally a female *U. tanneri* was feeding on this scat at the time of discovery). Tenebrionid beetles were found consuming deceased *U. tanneri*, and on one occasion a tenebrionid was discovered consuming a live *U. tanneri* that was actively trying to dislodge the beetle, without success.

There are undoubtedly other predators, both vertebrate and invertebrate, that could prey on adult or nymph *U. tanneri*. One such species is the longnose leopard lizard (*Gambelia wislizenii* (Baird and Girard)), a large species that was often encountered during this study. This species is a voracious consumer of invertebrates and small vertebrates; the diet in other parts of its range is often dominated by grasshoppers (Hammerson 1999). The northern scorpion (*Paruroctonus boreus* (Girard)) was frequently encountered at night, and also might take nymph *U. tanneri* due to their smaller size and nocturnal activity. Several species of birds might take *U. tanneri*.

On several occasions, individual *U. tanneri* were discovered dead on the surface of the sand, with most of these individuals still soft to the touch, indicating that they had recently expired and had not had time to dry in the arid climate. There was never any indication of predation on these individuals, rather it appeared that they had expired from other causes.

Adult *U. tanneri* seldom reacted to the approach of a human, even when followed in close proximity. Individuals usually only reacted to a human presence

when touched, whereupon they exhibited defensive behavior, usually fleeing a short distance via short hops, or lashing out with the spines on the metatibiae. Such behavior did not last long, and individuals ceased fleeing after one or two minutes. The lack of reaction to approach and visual stimulation is odd, considering that adult *U. tanneri* are conspicuous on the surface of the sand, and can be seen from considerable distance due to their black color against the lighter colored dunes.

In hand, *U. tanneri* will attempt to bite, kick with their hind legs in an attempt to drive the spines of the metatibia into the hand of the captor, and exude a viscous dark-colored regurgitate, which is a typical reaction of most Orthoptera when held.

DISCUSSION

Habitat

Figure 7 is meant to only be a rough representation of the distribution of dunes. Attempts to refine the classification of the landscape by using supervised Maximum Likelihood models were unsuccessful, even when training data were carefully selected from unsupervised classification results. Since *U. tanneri* occur on dunes and loose sand, the map might be used to investigate locations where *U. tanneri* have not yet been detected, but might occur due to the presence of dunes or loose sand. To date, no *U. tanneri* have been detected south or east of the Colorado River, which might indicate that this is a barrier to their dispersal.

I have confirmed *U. tanneri* in Emery, Garfield, and Wayne counties, mostly along the Utah state highway 24 corridor. Further investigation is needed to determine the range of *U. tanneri*, especially in areas of suitable habitat east of the Green River and Colorado River. The records from the Escalante Desert in Garfield and Kane counties need to be substantiated as well. In addition, the Coral Pink Sand Dunes require investigation, as there is a species of *Ammobaenetes* that occur on those dunes, and the habitat appears suitable to support populations of *U. tanneri*.

The habitat choice of *U. tanneri* has not been adequately quantified. Areas that appeared as likely habitat, such as Plot 2, occasionally had very few individuals, or no individuals were detected at all. I had examined the soil bulk densities among the plots to determine if this was a factor in habitat choice, but the bulk densities were similar. Therefore, the bulk density of the soil might not influence the

observed differences in cricket abundances among plots. More samples across more habitats are needed to determine if bulk density is a factor in cricket occurrence. Other soil factors might be important, specifically grain size, but this was not examined.

While mark and resight analysis indicated the mean abundance in Plot 1 was greater (483 individuals) than in Plot 2 (only one individual seen) and Plot 3 (50 individuals), this data can not be used to determine the habitat with the greatest abundance of *U. tanneri* because only one plot of each habitat type was examined, so the results can not be statistically compared. In addition, this data cannot assist in interpreting habitat quality, as the reproductive success of *U. tanneri* in the three study plots is unknown. There are several reasons multiple plots were not analyzed, namely because the sampling effort was too great for a single individual, and because time was limited. The abundance of crickets relative to site characteristics such as vegetation structure (i.e. canopy cover or species composition) and soil factors (i.e. grain size, soil moisture, or the presence of cryptobiotic crusts) should be investigated in further studies. The response of crickets to the movement of dunes across the landscape should also be examined.

Mark and Resight

There are some potential issues within the mark and resight analysis that relate to the assumptions of the mixed logit-normal model. This model does not require individually distinguishable marks on individuals, but does require sampling without replacement (McClintock 2013). Crickets were not physically

collected during each sample period, which would ensure sampling without replacement, because of the effort required to capture and detain numerous crickets during each transect. Instead, a straight transect was made through the center of the plot (Fig. 3), and only crickets located in front of the observer along this path were recorded. An effort was made to move constantly so that as a cricket was recorded, the observer passed beyond the location of the cricket and it was no longer in the field of vision. Some individual crickets were possibly counted multiple times (i.e., with replacement), especially unmarked individuals, but this was most likely an infrequent occurrence.

Another possible issue with the mark and resight analysis is a violation of the closed population assumption. Due to the remoteness of the field sites and the lack of available materials in nearby towns, it was impractical to build enclosures that ensured closed populations. To reduce the violation of this assumption, the data gathering period was short, about three hours between the start of marking individuals to the conclusion of the last transect; this was meant to reduce the immigration and emigration of individual crickets. While walking transects, marked individuals were seen within several meters of the boundary of the study plots on either side. Individuals within the plot were counted as resightings, while those outside the plot were not recorded. Unmarked individuals outside the plots were not recorded. However, encountering marked individuals outside the study plots was not common. Marked individuals were rarely found more than a few meters from the study plots, even days after initial marking (see below). When there is

equal immigration and emigration, the abundance calculated for the plot is considered to be an estimate of the superpopulation of crickets on the plot and the immediate surrounding area (McClintock 2013). The abundance for each plot might therefore be slightly overestimated compared to the abundance of the same area if the population was truly closed. This overestimation should be taken into account when examining the results of this study, though the impact of this violation was probably minor. The single individual recorded during the survey of Plot 2 was most likely an immigrant, as it was found in the southwest corner of the plot, where a small portion of loose sand entered the plot area from a dune that lay outside the plot. This individual was not detected again during the remainder of the sampling of this plot, and possibly emigrated out of the plot. Because of the lack of individuals within Plot 2, the mark and resight analysis could not be completed for Plot 2.

The sampling design of two subordinate transects in an "X" pattern assisted in meeting the assumption of sampling without replacement, but may have introduced an issue with non-independent sampling. Sampling was heaviest in the center of the plot where the transects overlapped, which reduced the randomness of individuals encountered.

While mark and resight data for each plot were recorded so that male and female results could be computed separately and compared to provide sex ratios, the results generated by Program MARK for female abundances were variable and unrealistically large, often returning numbers that suggested that millions of crickets occurred on each plot. This was probably an artifact of a small sample size,

and therefore male and female data were considered jointly to provide a larger sample size and a more robust analysis. The standard errors for the mark and recapture estimates of abundance are large (Table 9), even with the combined datasets. It is possible that because *U. tanneri* spend much time in their burrows, individuals entering or emerging from burrows during the transect counts could increase the variability in detection probability. This could not be calculated due to the lack of individually distinguishable marks on the crickets.

Individuals that were marked in Plot 1 before the final mark and recapture study to test methods for marking were observed for a week to determine paint durability. Over this period, few individuals were observed more than a few meters from the plot, with the individual observed the furthest from the plot being found approximately 20 m from Plot 1. The final mark and resight procedure used a different color mark than the original marks. Some individuals had two different colored marks during the final survey. Those individuals bearing only the original color were considered unmarked, and no special attention was given to those with two different colors.

During the marking process, individual crickets reacted to the application of paint to their thorax in different manners. Some individuals ignored the paint, some fled the site when touched, while others attempted to clean the paint off of their body by rolling on their backs in the sand. Occasionally crickets would draw their legs up over the thorax while the paint was applied, or would draw their forelimbs over the applied area. Both of these behaviors caused paint to be applied to the legs.

Most individuals attempted to clean paint off of the legs by grooming the legs with their mouths, and many engaged in the rolling behavior previously mentioned. Regardless of the reaction to the marking process, most marks remained visible for up to two weeks, even those initially covered with sand by rolling (these usually had sand caked into the paint mark). In addition, marked crickets quickly resumed normal behavior, and marked individuals were seen foraging, mating, and constructing burrows.

Behavior

During my effort to track a single individual through its daily activity, I attempted to mark several crickets with paint as they emerged from their burrow, in order to make tracking a particular individual easier. However, I deemed this deleterious to normal behavior, as the act of marking the cricket usually caused the cricket to react to the paint, which disrupted observations on behavior that would normally occur directly after emergence. Because individuals were unable to be marked, tracking an individual from emergence until cessation of surface activity proved to be difficult, as I soon lost track of individuals when several crickets would interact, especially if these interactions took place in vegetation. Because of this, only one individual was tracked long enough to gather substantial data, although I eventually lost this individual among several other individuals within a large purple sage.

There is probably only one generation of *U. tanneri* produced each year. No nymphs were observed from early May until early June, when 1st instars were

initially detected. Final instars are seen in late April (Tim Graham, personal communication, personal observation), and adults are last detected on the surface from mid to late July (Tim Graham, personal communication); Tinkham (1970) failed to find any *U. tanneri* during a collecting trip in late July 1970. It is unknown whether subterranean activity takes place after adults are no longer seen on the surface.

The time that crickets cease surface activity and enter burrows might be linked to increased predation pressure, rather than temperature, especially given the wide range of temperatures when crickets began to burrow. Lizards were rarely active during the peak activity of *U. tanneri*; however, lizards were frequently seen after 0900 hours, when most *U. tanneri* are constructing burrows.

The defensive behaviors of *U. tanneri* need additional investigation. The resemblance between *U. tanneri* and the sympatric *Eleodes caudiferus* LeConte and *E. obscurus* (Say) is strong (Fig. 13). Both *U. tanneri* and the sympatric *Eleodes* are black, approximately the same size, and have a similar gait. From a distance, it is difficult to distinguish between *Eleodes* and *U. tanneri*. Many *Eleodes* spp. are noxious, and the species sympatric with *U. tanneri* produce a disagreeable odor when disturbed, which can be detected from over a meter away (personal observation). Hetz and Slobodchikoff (1988) determined that when predators were presented with a noxious *Eleodes*, a palatable mimic, and a palatable non-mimic prey, the predators selected non-mimic prey at a higher rate than would be expected for an equal predation rate. They determined that mimics were consumed

at a level proportional to their abundance, but the noxious species were consumed much less than would be expected for equal predation rates. They concluded that some predators could distinguish between mimic and noxious species, although mimics still had a lower predation rate than did non-mimics, and, therefore, benefited from their mimicry. It is possible that this is the case with *U. tanneri*, as the scat of the coyote contained *U. tanneri* but no tenebrionids, even though they are frequently encountered on the surface at the same time as *U. tanneri*, and both would be available to a foraging predator. In addition, Cloudsley-Thompson (1991) suggested that black is a common aposematic coloration in desert ecosystems. This suggests that *U. tanneri* might be a Batesian mimic, though this cannot be determined conclusively without further studies.

Ecological Importance

Several authors have investigated food web interactions of rhaphidophorids in arid environments. Bradley (1983) based a small food web in New Mexico on *Ammobaenetes*, and demonstrated that even small webs can be extremely complex, which is supported by Polis (1991b), who emphasized that food web complexity is understated due to the lack of study on arthropods and because some authors omit species they are unfamiliar with and concentrate only on species of their expertise, or lump species into groups (Polis 1991a). Schoenly (1983) found *Ammobaenetes* associated with cattle dung. Crawford and Taylor (1984) suggested *Ammobaenetes* acted as a detritivore due to the presence of cellulose decomposing bacteria found in their gut, which occurred at a much higher level in the gut than in the surrounding

soil. In addition, Megías et al. (2011) found that macroarthropod detritivores have a large impact on the trophic interactions within arid ecosystems. The presence of *U. tanneri* in several scats and the observed predation indicate that *U. tanneri* is probably an important prey item for many species.

Like other species of sand treaders, *U. tanneri* is highly specialized for life in arid, sandy environments. *Utabaenetes tanneri* has a diverse diet that includes detritus, and likely has similar impacts to the ecosystem as *Ammobaenetes*. Unlike most other sand treaders, *U. tanneri* is diurnal which might relate to the dark coloration and Batesian mimicry unique to this species. In addition, their diurnal activity might explain its co-existence with *Ammobaenetes*, since the two species are using similar resources at different times. The studies on related species, the similarity of *U. tanneri* to other sand treader species, the high abundance of *U. tanneri*, and the presence of this species in the diet of several predators suggest that *U. tanneri* is an important component of the ecosystem where it occurs.

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Table 1. Plot 1 mark and resight raw data.

Transect	Marked Male	Marked Female	Unmarked Male	Unmarked Female
1 NW-SE	5	1	8	6
1 NE-SW	0	0	10	11
2 NW-SE	10	0	14	13
2 NE-SW	3	1	24	25
3 NW-SE	13	1	12	17
3 NE-SW	4	2	13	16
4 NW-SE	8	1	14	15
4 NE-SW	3	1	21	12
5 NW-SE	9	0	14	17
5 NE-SW	3	1	12	13
6 NW-SE	3	0	15	12
6 NE-SW	4	0	10	11
Total marked in population		54 males	12 females	

Table 2. Plot 3 mark and resight raw data.

Transect	Marked Male	Marked Female	Unmarked Male	Unmarked Female
1 NW-SE	2	3	1	0
1 NE-SW	3	0	0	1
2 NW-SE	2	0	1	0
2 NE-SW	0	0	3	4
3 NW-SE	2	0	1	0
3 NE-SW	3	0	3	2
4 NW-SE	2	0	0	1
4 NE-SW	0	0	4	2
5 NW-SE	2	0	2	1
5 NE-SW	1	1	3	4
6 NW-SE	2	1	1	1
6 NE-SW	1	2	9	2
Total marked in population		11 males	5 females	

Table 3. Program MARK encounter history file for Plot 1.

```
101111111111     3;
100111110100     1;
101010001000     2;
001011101001     1;
001010100000     4;
000010001000     3;
000001000000     1;
000000000000    66;

Unmarked Seen Group=1;

35 76 58 62 56 48;
```

Table 4. Program MARK encounter history file for Plot 3.

```
111011101111     1;
111011101010     1;
100000000110     1;
100000000001     2;
010001000000     1;
000000000000    10;

Unmarked Seen Group=1;

2 8 6 7 10 13;
```

Table 5. Selected measurements (in mm) of male *U. tanneri*.

					Min	Max	Mean	Std. dev.
Total length	18.60	18.14	19.22	16.28	16.28	19.22	18.06	1.27
Length pronotum	3.88	4.34	5.27	4.65	3.88	5.27	4.53	0.59
Width pronotum	6.36	6.67	7.60	6.82	6.36	7.60	6.86	0.53
Length abdomen	7.75	8.53	7.13	6.98	6.98	8.53	7.60	0.70
Width head	5.74	5.43	5.74	4.81	4.81	5.74	5.43	0.44
Width between antennae	1.12	1.18	1.18	1.18	1.12	1.18	1.16	0.03
Synthlipsis	2.73	2.85	3.08	2.43	2.43	3.08	2.77	0.27
Protarsal 1	1.14	0.87	1.25	0.80	0.80	1.25	1.02	0.22
Protarsal 2	0.19	0.23	0.38	0.15	0.15	0.38	0.24	0.10
Protarsal 3	1.90	1.71	1.90	1.82	1.71	1.90	1.83	0.09
Protibia	7.60	8.06	7.91	6.82	6.82	8.06	7.60	0.55
Profemur	7.13	7.13	7.29	6.51	6.51	7.29	7.01	0.34
Mesotarsal 1	0.87	1.29	1.22	1.14	0.87	1.29	1.13	0.18
Mesotarsal 2	0.25	0.65	0.53	0.49	0.25	0.65	0.48	0.17
Mesotarsal 3	0.25	0.30	0.30	0.30	0.25	0.30	0.29	0.03
Mesotarsal 4	1.30	1.37	1.48	1.33	1.30	1.48	1.37	0.08
Mesotibia	7.91	8.37	8.37	7.60	7.60	8.37	8.06	0.38
Mesofemur	6.82	7.44	7.60	7.13	6.82	7.60	7.25	0.34
Metatarsal 1	1.67	1.56	1.82	1.67	1.56	1.82	1.68	0.11
Metatarsal 2	0.23	0.27	0.34	0.27	0.23	0.34	0.28	0.05
Metatarsal 3	2.09	2.36	2.32	2.17	2.09	2.36	2.23	0.13
Metatibia	13.49	15.66	14.42	13.18	13.18	15.66	14.18	1.11
Metafemur	17.83	16.43	17.52	15.50	15.50	17.83	16.82	1.06
Ovipositor								
Longest sand basket spine	2.58	2.85	2.43	2.39	2.39	2.85	2.57	0.21
Shortest sand basket spine	1.37	1.37	1.44	1.10	1.10	1.44	1.32	0.15

Table 6. Selected measurements (in mm) of female *U. tanneri*.

							Min	Max	Mean	Std. dev.
Total length	18.14	19.38	16.28	14.73	17.05	17.05	14.73	19.38	17.10	1.59
Length pronotum	4.81	4.65	3.88	3.57	3.41	3.57	3.41	4.81	3.98	0.60
Width pronotum	7.29	7.13	6.51	5.89	6.51	6.05	5.89	7.29	6.56	0.56
Length abdomen	6.82	7.75	5.43	6.20	8.53	7.75	5.43	8.53	7.08	1.15
Width head	5.74	5.89	5.74	5.12	4.65	4.96	4.65	5.89	5.35	0.51
Width between antennae	1.09	1.14	1.10	1.06	1.06	1.22	1.06	1.22	1.11	0.06
Synthlipsis	2.95	2.85	2.74	2.51	2.36	2.66	2.36	2.95	2.68	0.22
Protarsal 1	1.03	1.22	0.72	0.91	0.84	0.80	0.72	1.22	0.92	0.18
Protarsal 2	0.38	0.23	0.19	0.34	0.30	0.38	0.19	0.38	0.30	0.08
Protarsal 3	1.75	1.82	1.56	1.75	1.60	1.60	1.56	1.82	1.68	0.11
Protibia	6.82	6.51	5.43	5.58	5.27	5.74	5.27	6.82	5.89	0.63
Profemur	6.32	6.20	5.12	5.27	5.58	5.89	5.12	6.32	5.73	0.49
Mesotarsal 1	1.18	1.14	0.95	1.10	0.95	0.91	0.91	1.18	1.04	0.11
Mesotarsal 2	0.38	0.53	0.27	0.49	0.46	0.42	0.27	0.53	0.42	0.09
Mesotarsal 3	0.23	0.19	0.19	0.30	0.34	0.34	0.19	0.34	0.27	0.07
Mesotarsal 4	1.33	1.37	1.03	1.25	1.29	1.29	1.03	1.37	1.26	0.12
Mesotibia	7.13	6.67	5.74	5.43	5.74	6.05	5.43	7.13	6.12	0.65
Mesofemur	6.39	5.74	5.58	5.27	5.27	5.43	5.27	6.39	5.61	0.42
Metatarsal 1	1.52	1.60	1.79	1.44	1.29	1.41	1.29	1.79	1.51	0.17
Metatarsal 2	0.19	0.23	0.27	0.30	0.30	1.44	0.19	1.44	0.46	0.49
Metatarsal 3	2.09	1.98	1.63	1.94	1.86	1.90	1.63	2.09	1.90	0.15
Metatibia	11.32	11.16	10.23	9.92	10.23	9.77	9.77	11.32	10.44	0.65
Metafemur	13.49	12.56	11.47	10.85	11.47	11.63	10.85	13.49	11.91	0.95
Ovipositor	11.32	10.23	10.70	10.08	9.30	9.61	9.30	11.32	10.20	0.73
Longest sand basket spine	4.46	3.42	2.48	2.66	2.17	2.66	2.17	4.46	2.98	0.84
Shortest sand basket spine	1.30	1.22	1.30	1.14	1.14	1.33	1.14	1.33	1.24	0.09

Table 7. Bulk densities of mark and resight sample plots in g/cm^3. σ = standard deviation.

	Bulk Densities		
Sample	Plot 1	Plot 2	Plot 3
1	1.51	1.57	1.85
2	1.69	1.60	1.77
3	1.68	1.53	1.56
4	1.55	1.58	1.55
5	1.59	1.56	1.53
6	1.52	1.61	1.53
7	1.52	1.49	1.60
8	1.52	1.73	1.65
9	1.60	1.54	1.45
10	1.61	1.50	1.41
11	1.59	1.64	1.81
12	1.51	1.51	1.43
13	1.60	1.54	1.58
14	1.62	1.64	1.55
15	1.71	1.54	1.78
16	1.61	1.51	1.59
Mean	1.59	1.57	1.60
σ	0.07	0.06	0.14

Table 8. Activity of a single male *U. tanneri* during the morning of 8 June 2013. DOM = drive off male, RTB/E = return to burrow and excavate, DABM = driven off by rival male, ATM/F = attempt to mate and fail. Food items: 1) Indian ricegrass (*A. hymenoides*), 2) purple sage (*P. incana*), 3) resinbush (*C. stylosus*). The individual was lost in a group of several individuals after 6:43:20.

Time	Behavior	Time	Behavior
5:28:00	Emerge	5:57:00	Move
5:29:00	Sit	5:59:30	Sit
5:32:00	Move	6:00:20	Move
5:35:00	Sit	6:00:30	Sit/Rotate
5:35:00	Eat[1]	6:02:20	DOM
5:35:00	Move	6:02:25	Move
5:35:00	Eat[1]	6:02:50	DOM
5:36:56	Move	6:02:52	Sit
5:37:00	DOM	6:03:00	Move
5:37:50	Sit	6:06:45	Sit
5:38:00	Move	6:07:25	Move
5:39:05	Sit/Rotate	6:08:00	Sit
5:39:30	Move	6:08:27	DOM
5:41:20	Sit	6:08:32	Sit
5:42:00	Move	6:10:06	Eat[2]
5:42:15	RTB/E	6:10:49	DOM
5:43:43	Emerge	6:10:54	Sit
5:46:00	Sit	6:11:20	Move
5:46:51	Move	6:15:38	Eat[2]
5:48:16	Sit	6:16:00	Move
5:48:55	Move	6:17:06	Sit
5:49:20	Sit	6:17:25	Move
5:50:10	DOM	6:20:07	Eat[3]
5:50:20	Sit/Rotate	6:23:15	Move
5:53:18	Move	6:26:47	Eat[2]
5:53:30	Sit	6:28:37	Move
5:54:13	Move	6:31:50	Sit
5:54:45	DABM	6:33:15	Move
5:55:15	Move	6:43:20	Sit
5:56:45	ATM/F		

Table 9. Results of mark and resight analyses for the six major sampling efforts (transects) in Plot 1 and Plot 3. Plot 2 did not have enough data to compute estimated abundances. Upper and lower estimates are 95% confidence intervals. σ = standard deviation.

	Transect	Abundance Estimate	Standard Error	Lower Interval	Upper Interval
Plot 1	1	544	214.24	92	997
	2	517	143.38	169	864
	3	313	67.68	143	483
	4	463	131.68	148	778
	5	426	118.03	150	702
	6	629	243.43	97	1161
	Mean	482			
	σ	108.36			
Plot 3	1	19	2.22	15	24
	2	75	44.91	0	164
	3	34	10.40	12	55
	4	67	39.53	0	146
	5	54	22.28	8	100
	6	49	16.17	15	84
	Mean	50			
	σ	20.67			

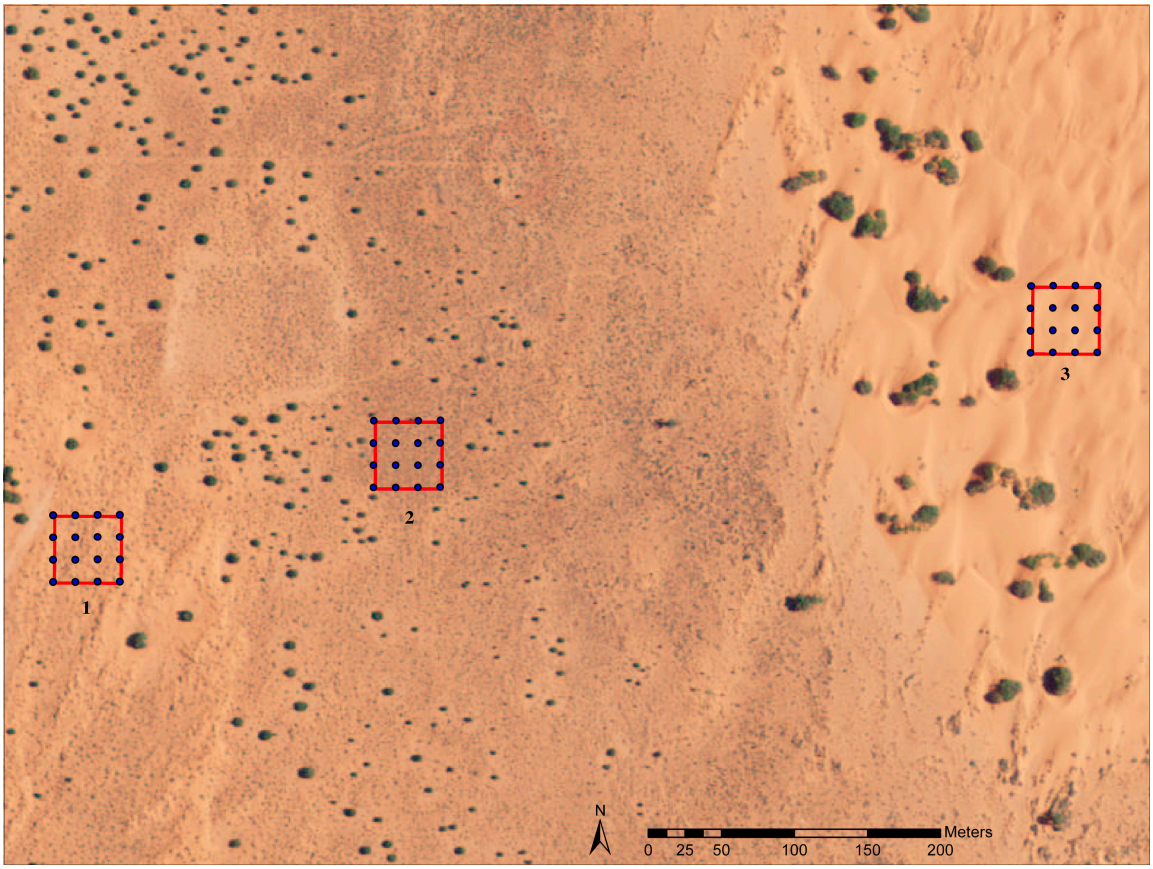

Fig. 1. Location of study plots in Garfield County, UT. Left is Plot 1, center is Plot 2, and right is Plot 3. Dots indicate soil sample locations. The landscape-scale differences between the plots are apparent in this image, especially in color. Soil bulk density failed to account for this observed difference, as the plots all had similar bulk densities. Airphoto is from 2011 National Agricultural Imagery Program.

Fig. 2. Example paint marks used for mark and resight. Left: female *U. tanneri* from Plot 3 showing red mark. Right: Male from Plot 1 showing blue mark. Different color marks were used in order to assess which plot an individual was marked in originally.

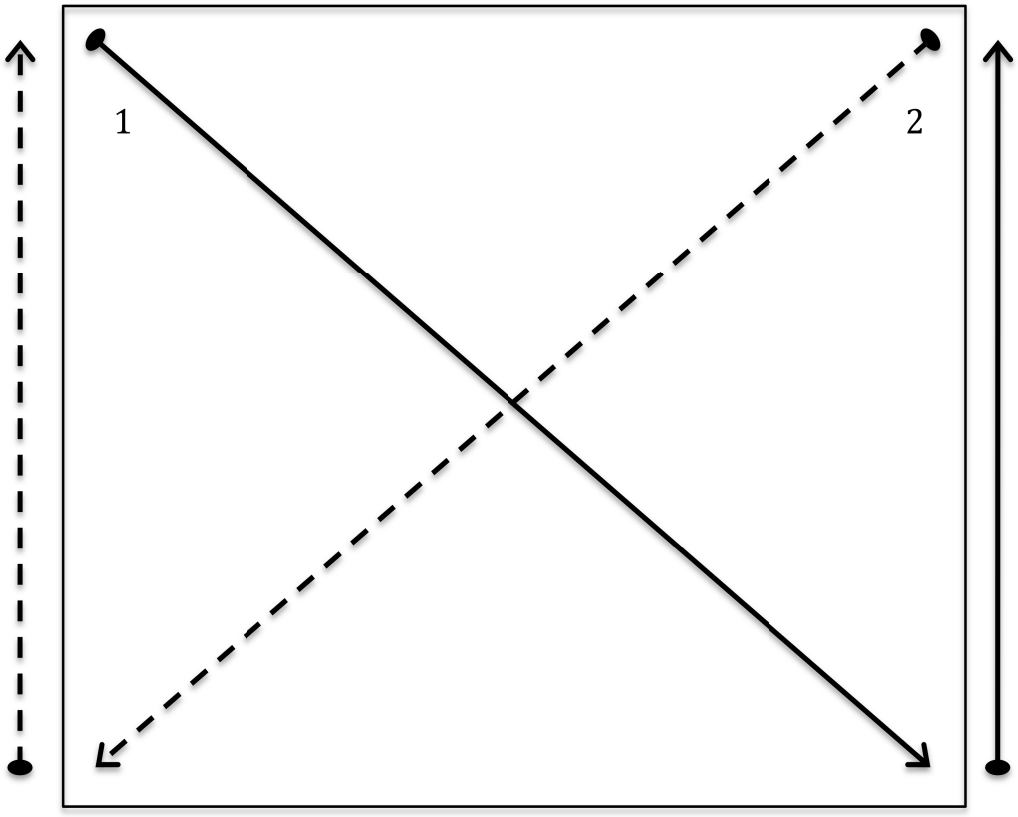

Fig. 3. Diagrammatic representation of sampling protocol for mark and resight. The observer starts in the northwest corner of the plot, and samples along the first transect (1). The observer then traverses outside the plot to the northeast corner, and samples along the second transect (2). The observer then returns to the start position by traversing outside the plot.

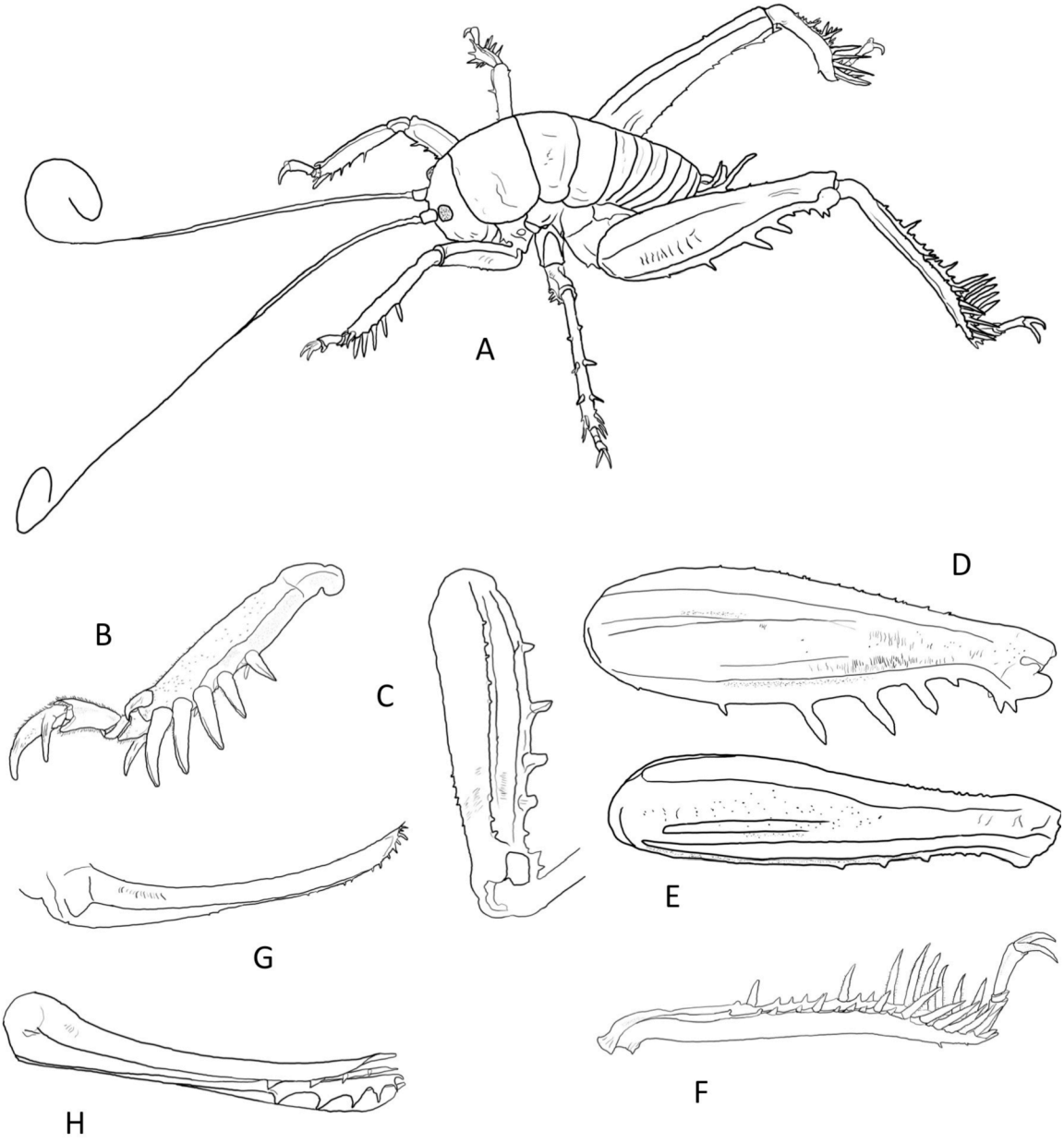

Fig. 4. Drawings of selected anatomical features of *U. tanneri*. A) male *U. tanneri*; B) posterolateral view of right protibia and protarsi of female; C) ventral view of right metafemur of male showing large posterior spines; D) posterolateral view of right metafemur of male; E) posterolateral view of right metafemur of female; F) posterolateral view of right metatarsi and metatibia of male showing sand basket; G) left lateral view of ovipositor; H) left lateral view of ovipositor showing both upper and lower valvulae.

Fig. 5. The eyes of *U. tanneri* are sexually dimorphic: eyes of males (left) are golden in color, while those of females (right) are black.

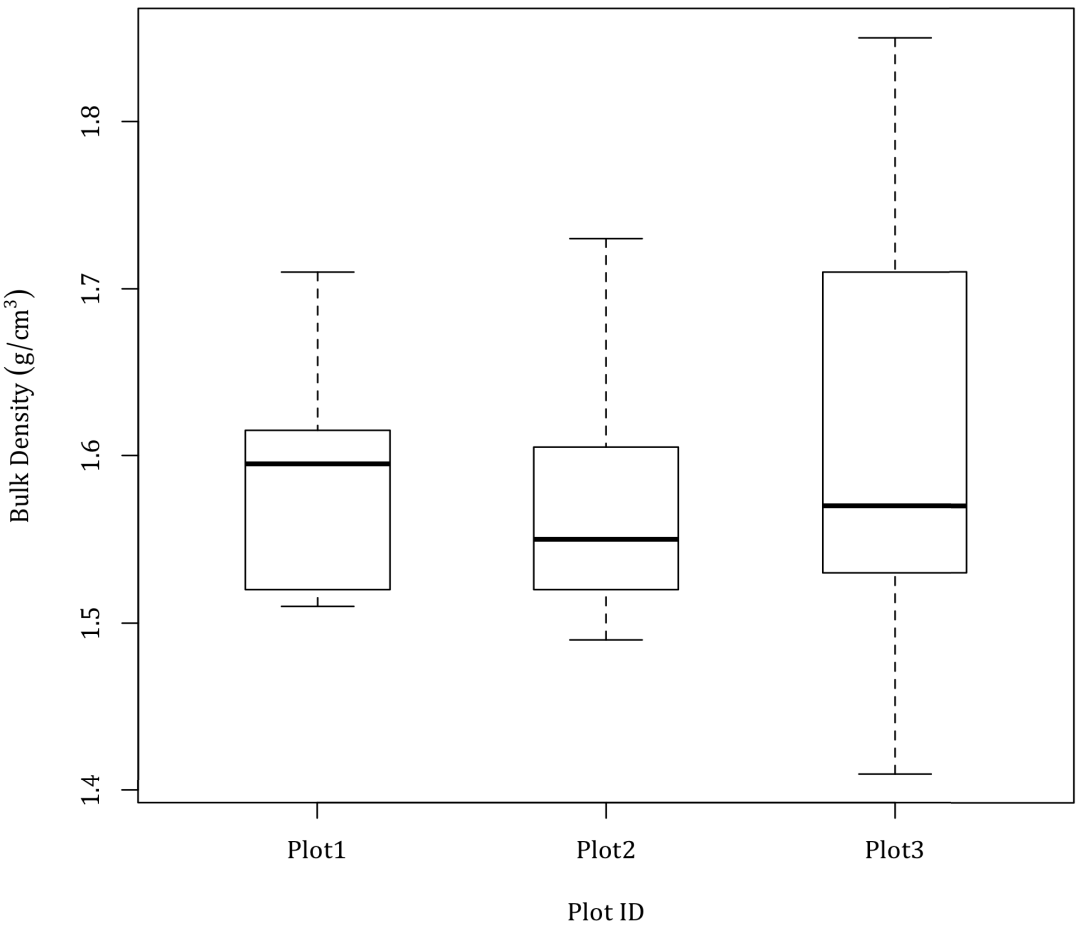

Fig. 6. Box and whisker plot of soil bulk density depicting range (whiskers) and median (black bars). Boxes depict 50% of the data, with 25% above the line, and 25% below.

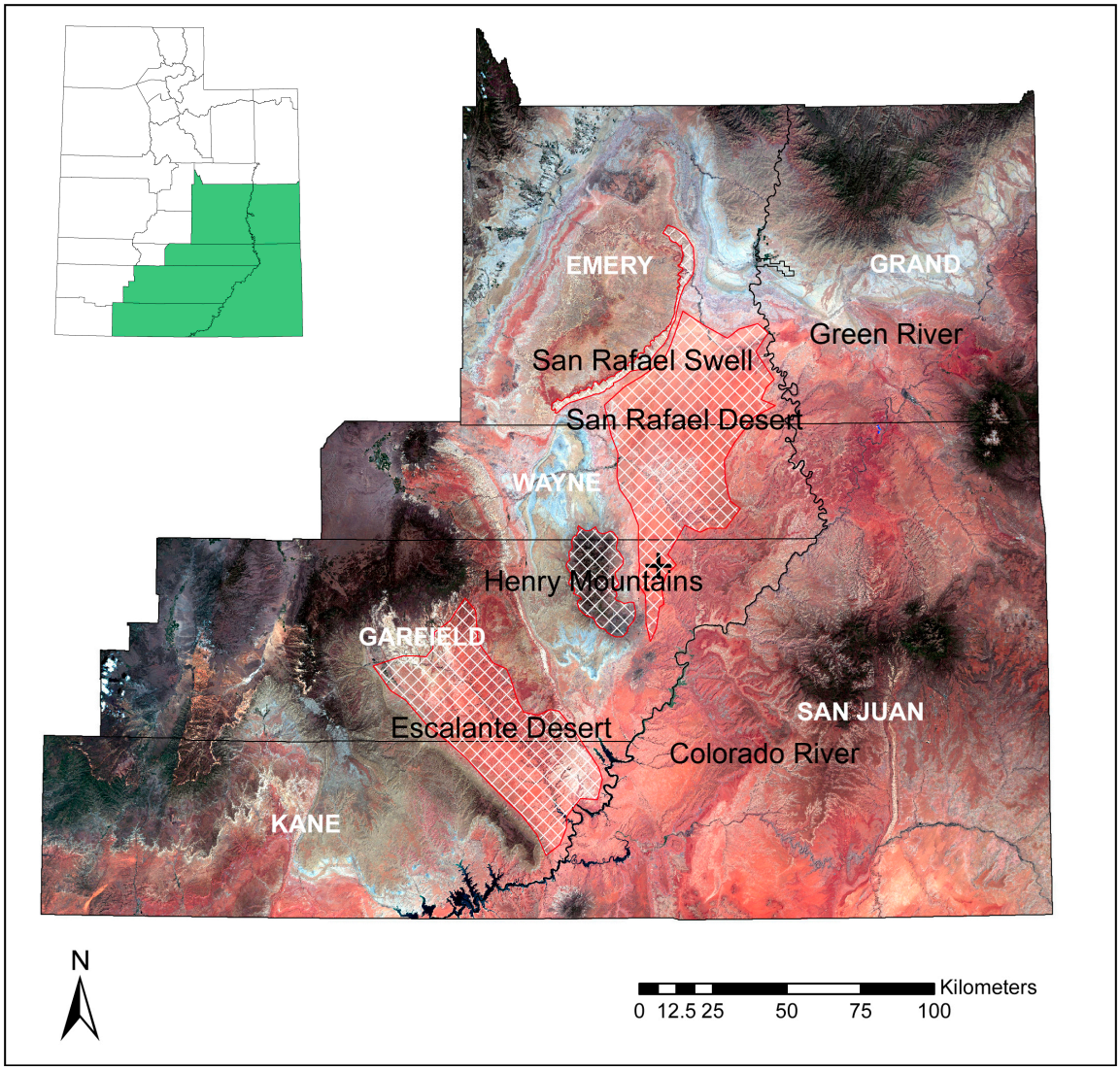

Fig. 7. Notable geographic features in southeast Utah that are located around the study area. The white crosshatched areas roughly outline the deserts, the San Rafael Swell, and the Henry Mountains. The location of the mark and resight study plots is indicated by the black "+" symbol. LandSat 8 imagery acquired from the United States Geological Survey. County and state maps acquired from the Utah Automated Geographic Reference Center.

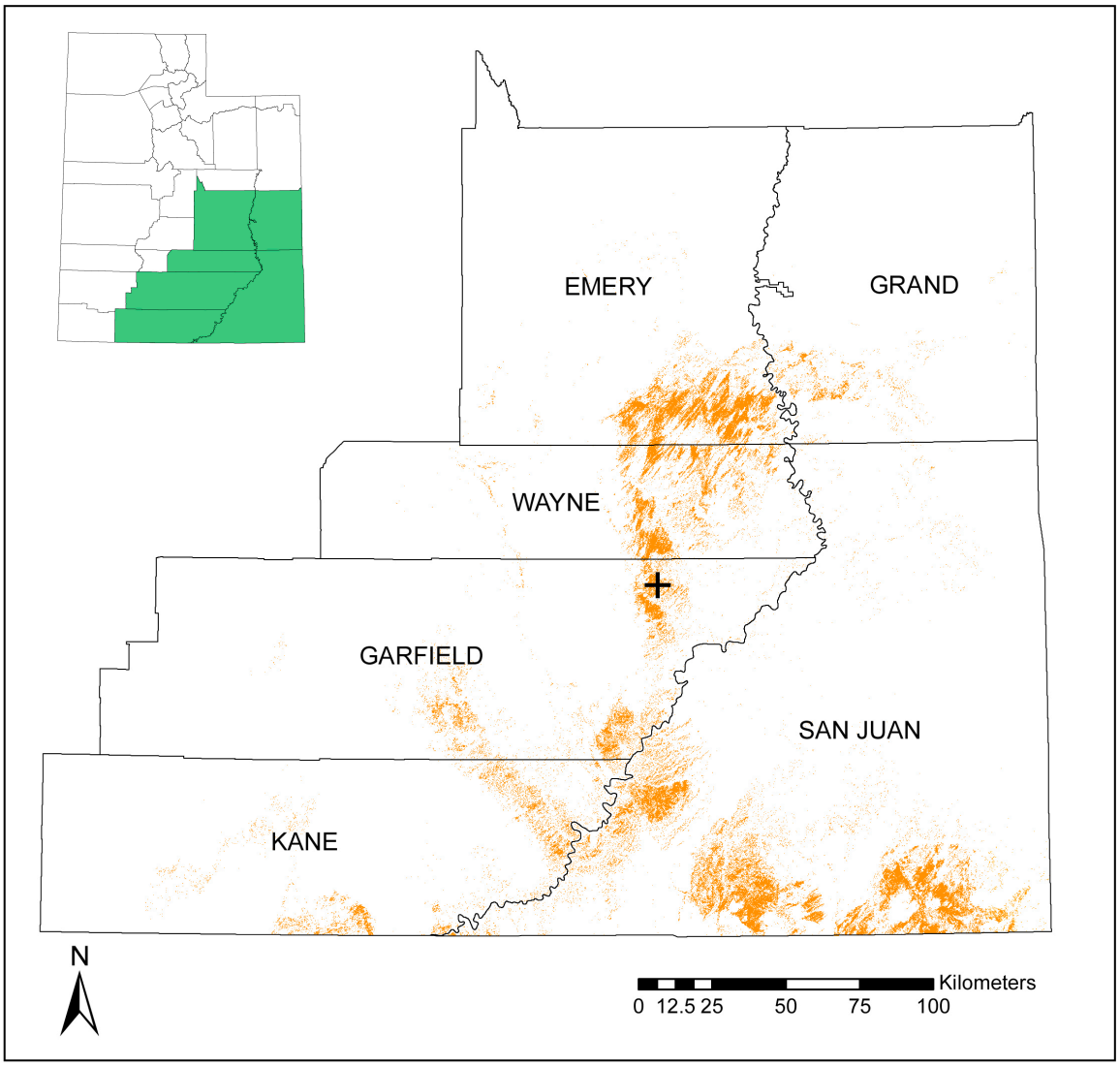

Fig. 8. Distribution of sand dunes and other loose, bare, sand in southeast Utah. The areas indicated on the map would be areas of interest when surveying for *U. tanneri*. The location of the mark and resight study plots is indicated by the black "+" symbol. Source data for analysis from LandSat 8 imagery acquired from the United States Geological Survey. County and state maps acquired from the Utah Automated Geographic Reference Center.

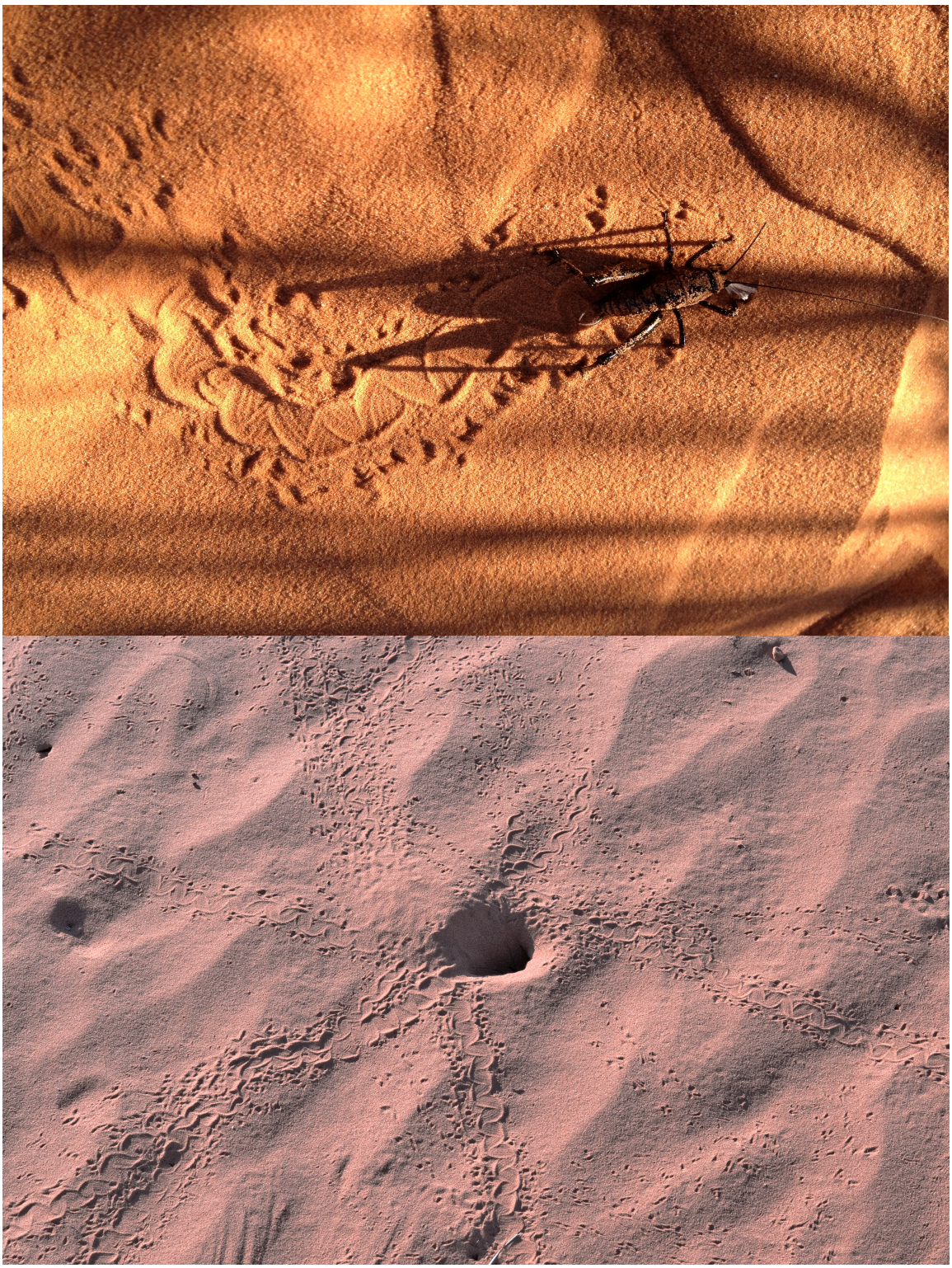

Fig. 9. Specialized male tracks in progress (upper) and surrounding a burrow (lower).

Fig. 10. Captive late instar *U. tanneri* constructing a burrow. The burrow plug is located behind the cricket.

Fig. 11. Male (left) and female (right) *U. tanneri* engaging in copulation.

Fig. 12. Coyote (*C. latrans*) scat predominantly containing remains of *U. tanneri*. The knife is 5.71 cm in length.

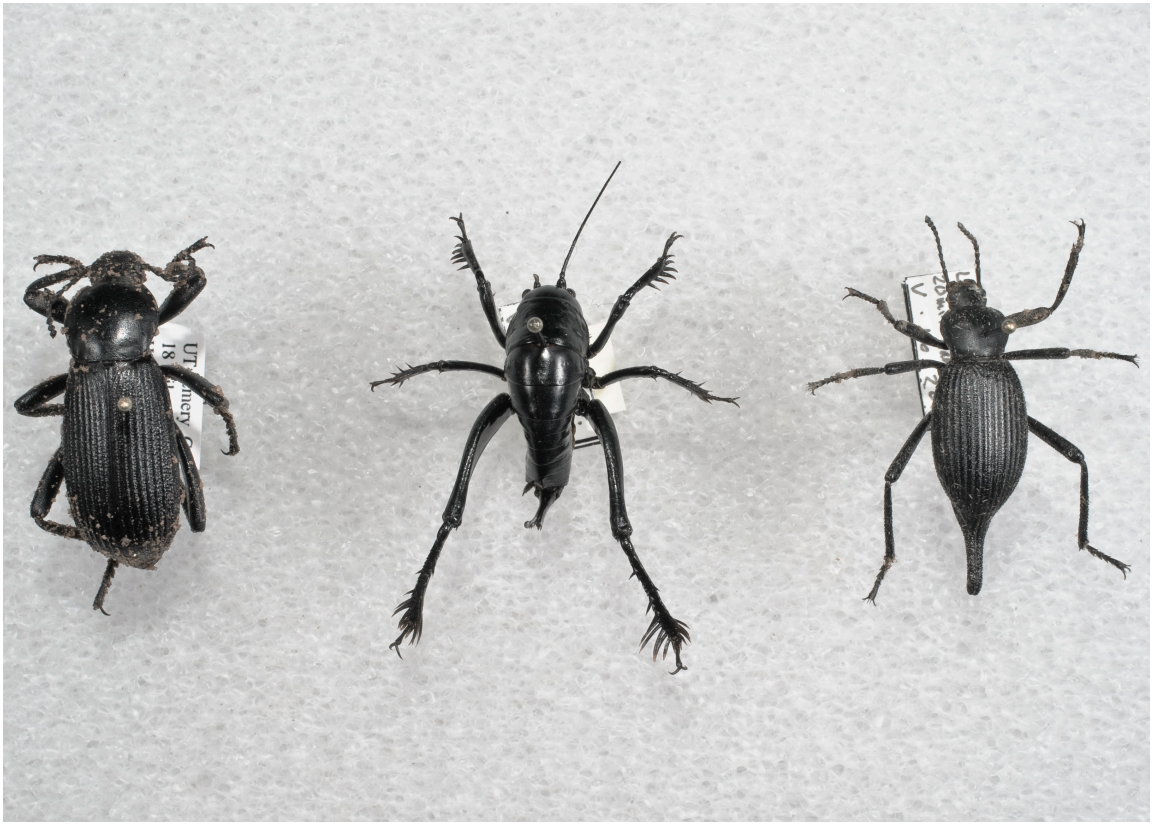

Fig. 13. Photograph of pinned specimens of *Eleodes obscurus* (left), *U. tanneri* (center), and *E. caudiferus* (right) illustrating the similarity of the appearance of *U. tanneri* to the noxious tenebrionids.